THE COLOR SENSE OF THE HONEY-BEE: THE POLLINATION OF GREEN FLOWERS[1]

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CARL NAGELI, in a memoir often cited, after stating the common opinion that insects are especially attracted by the bright coloration of floral organs, says: "We understand now why there are no green flowers; they would be invisible in the midst of foliage."

We seem to dream when we read these lines written seriously by a naturalist. As the lists below demonstrate, not only are there a large number of green or greenish flowers, invisible or scarcely visible in the midst of foliage, but insects discover them without the least difficulty.

This false notion of the non-existence of green flowers, which can only be excusable among those unacquainted with botany, has arisen from many causes; the plants which bear flowers of this nature are only cultivated when they are of medicinal use or are valuable for food, when they are frequently regarded as vegetables rather than as flowers. In foreign countries natural history collectors travelling for horticulturists disdain everything which has not at least a decorative foliage. Furthermore, the authors who attach great importance to the coloration of the floral envelopes for the attraction of insects have often neglected to mention in their works that such and such a species, though fertilized by winged arthropods, possesses green or greenish flowers. H. Müller has committed this fault many times, and Charles Darwin in his celebrated work on the fertilization of orchids passes over the color usually in silence.

A reaction was necessary; it was important to remind biologists that there exists a long series of green flowers, greenish, or scarcely visible, which insects find as easily as the others, despite the absence of their so-called attractive colors.[2]

Plateau then proceeds to enumerate 91 entomophilous species, of which 41 had green or largely green flowers,

[1] "The Color Sense of the Honey-bee: Is Conspicuousness an Advantage to Flowers?" AMER. NAT., 43, 338–349, June, 1909; "The Color Sense of the Honey-bee: Can Bees Distinguish Colors?" AMER. NAT., 44, 673–692, November, 1910.

[2] Plateau, F., "Comment les fleurs attirent les insectes," 4me partie, *Bull. Acad. roy. Belgique*, 3me série, 34, 614–615, 1897. In the writer's opinion, whenever Müller or Darwin omits to mention the color of a flower, it is either through inadvertence or because it is assumed to be well known.

38 greenish and 12 brownish or brown flowers, to the larger part of which insect visits had been observed by himself or other floroecologists. Of 72 of these forms he examined the color himself and observed insect visits to 63 of them, or more than two thirds. Plateau believed that the visits of insects to green flowers very strongly supported his views, and in one of his last papers on the pollination of *Listera ovata,* an orchid with green flowers, he again returns to this subject. In a letter to the writer he states that he had made innumerable observations on the pollination of green flowers, which had extended over twelve years. His conclusion as finally expressed is as follows:

> It is not the colors more or less bright of the corollas but other causes which guide to flowers their winged pollinators. Green or greenish flowers notwithstanding their hue similar to that of foliage are as effectively fertilized by insects as white, blue, red, or yellow flowers, consequently, all these floral colorations might disappear from nature without the pollination and reproduction of plants being diminished.[3]

It is desirable to examine briefly the pollination of green flowers and to consider whether this conclusion is sustained or not.

A familiar example of a yellowish-green flower attractive to insects is offered by the garden asparagus (*Asparagus officinalis*). The flowers are mellifluous, pleasantly scented and frequented by honey-bees and less often by smaller species of bees. Müller says that "in spite of their inconspicuous color they are easily visible at a distance"; but Plateau describes them as "peu visible," an illustration perhaps that an observer is apt to be influenced by his point of view as well as by the color of the flower. As the result of personal trial I find that they can be distinctly seen at a distance of at least fifty feet. Another yellowish-green flower is *Tilia ulmifolia,* or basswood, which, according to both Müller and Plateau, is sought by honey-bees in immense numbers. This is also true of the American basswood (*Tilia ameri-*

[3] Plateau, F., "La pollination d'une orchidée a fleurs vertes '*Listera ovata* R. Br.' par les insectes," *Bull. Soc. roy. Belgique,* 46, 339, 1909.

cana), which, according to Root, an eminent authority on American apiculture, furnishes more honey than any other plant known, with perhaps the single exception of the white clover.[4] Other greenish, or dull-colored flowers, which the honey-bee was observed to visit were *Ampelopsis quinquefolia, Teucrium Scorodonia, Comarum palustre, Atropa Belladonna,* and several species of *Scrophularia.*

But of the 91 greenish or brownish hued species the honey-bee was seen to visit only 27, that is, there are no recorded visits of this bee to a little over seventy per cent. of the listed flowers. To four species there are no records of the visits of any insect. The remaining species were chiefly visited by flies, sometimes minute species, beetles, and the less specialized Hymenoptera; but *Hedera helix* was attractive to wasps and *Platanthera bifolia* to Lepidoptera. How meager the number of visits was should be noted: *Celastrus Orixa* was visited only by the domestic fly and one other species of Diptera; *Alchemilla hybrida* only by small Muscidæ; *Alchemilla alpina* in the Alps by one beetle and two Muscidæ; *Alchemilla fissa* in the same mountains by three Muscidæ; the sessile green flowers of *Herniaria glabra* were visited only by very small insects; the yellowish-green flowers of *Amarantus retroflexus* by the domestic fly and one beetle; *Lepidium Smithii* by small flies and many beetles of the genus *Altica; Angelica pyrenæa* by one beetle and two flies; three species of *Euphorbia* were visited only by flies; *Salsoda Soda* by *Syritta pipiens* and microscopic Diptera; among brownish flowers *Pelargonium triste* was visited by one fly; *Vincetoxicum purpurascens* only by *Musca domestica;* the brown-violet flowers of *Veratrum nigrum* and the reddish flowers of *Neottia Nidus-avis* only by flies. According to this list, in a few instances greenish flowers secreting nectar very freely are visited by a large number of insects, but the majority of the species are evidently not well adapted to entomophily.

[4] Root, A. I., "The ABC of Bee Culture," p. 38, 1903.

This conclusion is sustained by an examination of the green flowers of eastern North America. In the territory east of the 102d meridian and northward of North Carolina and Tennessee there are 1,244 green or dull colored flowers, of which 1,021 are anemophilous or hydrophilous, while 223 are entomophilous or autogamous. The wind-pollinated flowers are small and usually greenish, as in the 705 species of grasses and sedges, from which the inference is commonly drawn that anemophily and inconspicuousness are correlated. In the few exceptions (about 27 in the flora of the eastern states) where anemophilous flowers have brighter hues, as in the golden yellow aments of the yellow birch and the deep red panicles of the field sorrel (*Rumex Acetosella*), the colors of the small flowers are usually determined by the production of yellow or red pigments in great abundance by the vegetative organs—the entire plant of the field sorrel being sometimes red-colored.

Of the 223 green flowers, which are entomophilous or autogamous, many have no petals, as fifteen species of the Polygonaceæ and eight species belonging to the Caryophyllaceæ, also in several Rosaceæ, in *Acer saccharinum* and *Didiplis diandra*. Many are self-fertilized, as *Triglochin* and *Scheuchzeria,* and the orchids *Habenaria hyperborea* and *Epipactis viridiflora,* and the small green flowers of *Lechea* and *Penthorum sedoïdes*. Some have the petals caducous and depend upon their scent to attract insects, as the Vitaceæ. Many are visited chiefly by flies and the smaller bees, as various Melanthaceæ, the Smilaceæ, and the green flowers of the Asclepiadaceæ. A few species secrete nectar freely and attract numerous visitors, as the rock maple, basswood and the dark green pistillate flowers of *Rhus typhina*. Large green flowers, which are fragrant, nocturnal and are pollinated by moths, are found in exotic Solanaceæ and Orchidaceæ. It is obvious that bright coloration is less important to moth flowers than a strong scent, since red and blue

shades are invisible at night. But as a whole green flowers are small or even minute and attract few insects.[5]

Since in Europe and America, where the insect fauna is rich both in species and individuals and the flora displays a great variety of brilliant hues and delicate shades, dull-colored flowers are not well adapted to entomophily, it may be inferred that in a country where the flowers are largely greenish there would be a scarcity of anthophilous insects. According to A. R. Wallace and G. M. Thomson this condition is partially realized in the Islands of New Zealand. Wallace says:

In New Zealand where insects are strikingly deficient in variety the flora is almost as strikingly deficient in gayly colored blossoms. Of course there are some exceptions, but, as a whole, green, inconspicuous and imperfect flowers prevail to an extent not equalled in any other part of the globe, and affording a marvellous contrast to the general brilliancy of Australian flowers, combined with the abundance and variety of its insect life. We must remember, too, that the few gay or conspicuous flowering-plants possessed by New Zealand are almost all of Australian, South American, or European genera. . . . After the preceding paragraphs were written, it occurred to me that, if this reasoning were correct, New Zealand plants ought to be also deficient in scented flowers, because it is part of the same theory that the odors of flowers have, like their colors, been developed to attract the insects required to aid in their fertilization. I therefore at once applied to my friend Dr. Hooker, as the highest authority on New Zealand botany; simply asking whether there was any such observed deficiency. His reply was, New Zealand plants are remarkably scentless.

After quoting the above passage, G. M. Thomson, who resided in New Zealand and made a special study of its floroecology adds:

It is impossible to differ from this reasoning in toto, because the statements and facts on which it is founded are to a great extent correct, though in the light of more recent knowledge they require considerable modification.[6]

Bees and butterflies, according to Thomson, are comparatively rare; while Diptera, of which it is estimated

[5] Lovell, John H., "The Colors of Northern Gamopetalous Flowers," Amer. Nat., 37, 365–384 and 443–479.

[6] Thomson, G. M., "On the Fertilization of New Zealand Flowering Plants," *Trans. Proc. N. Z. Inst.*, 13, 241–288, 1880; Wallace, A. R., "The Geographical Distribution of Animals," 1, 457–464.

there may be a thousand species, are here the chief agents in the pollination of flowers, whereas in America and a large part of Europe they occupy the second place and in the Alps the third place. Neither honey-bees nor bumble-bees were found in New Zealand at the time of its discovery.

The phylogenetic history of green flowers likewise strongly supports the view that they are not well adapted to pollination by insects. In the opinion of many eminent botanists all greenish, inconspicuous flowers have been derived by retrogression from larger entomophilous ancestors. This theory has been very ably developed by Professor C. E. Bessey in his taxonomy of the Angiosperms, for which he suggests the restoration of the more appropriate name of Anthophyta. The buttercups (Ranales), the water plantains (Alismales) and roses (Rosales) are regarded as primitive and are placed at the beginning of the Anthophyta. The typical flower was entomophilous, of large size, and its organs were separate and spirally arranged. Engler's spiral series of Monocotyledons, which is composed of orders mostly devoid of a perianth, is derived from a liliaceous type; while the Apetalæ are treated as reduced forms and distributed among the petalous Dicotyledons.[7]

A similar view is adopted by Arber and Parkin in their discussion of the origin of Angiosperms. They reach the conclusion "that the Apetalous orders without perianth, such as the Piperales, Amentiferous families and Pandanales, can not be regarded as primitive Angiosperms, but have been derived from ancestors with a well-developed perianth. Entomophily . . . has supplied the 'motive force,' which not only called the Angiosperms into existence, but laid the foundation of their future prosperity."[8] Even if Engler's system of classification

[7] Bessey, Charles E., "The Phylogeny and Taxonomy of Angiosperms," *Bot. Gaz.*, 24, 145–178, 1897; "A Synopsis of Plant Phyla," *University Studies*, 7, 275–373, 1907; "The Phyletic Idea in Taxonomy," *Science*, 29, 91–100, 1909, etc.

[8] Arber, E. A. Newell, and Parkin, John, "On the Origin of Angiosperms," *Journal of Linnean Society* (Botany), 38, 29–80, 1907.

is accepted and the apetalous orders be regarded as primitive it does not support the thesis that small, green flowers are at no disadvantage in attracting insects because of their inconspicuousness. That reduction and change from entomophily and conspicuousness to anemophily and inconspicuousness has occurred repeatedly in widely separated families is not questioned by any ecologist or taxonomist. This is illustrated by the genera *Artemisia, Ambrosia,* etc., among the Compositæ; in *Ricinus* of the Euphorbiaceæ; probably also in the family Juncaceæ, and in species of *Thalictrum, Fraxinus, Sanguisorba* and *Poterium.* The evidence supplied by the phylogeny of green flowers is wholly in favor of the value of color contrast for gaining the attention of insects.

Approaching the problem from another direction, the Rev. George Henslow in his work on the self-fertilization of plants finds that "inconspicuous flowers are almost invariably self-fertilizing, or else inconspicuous."

> There are several reasons why inconspicuous flowers are not likely to be intercrossed by insects: (1) Their unattractiveness; (2) the absence of honey-secreting organs; (3) the want of scent; (4) they frequently do not expand, or at most remain half open, especially in cold or inclement weather, while perfectly cleistogamic flowers are, of course, never open; (5) their structure sometimes would seem absolutely to prevent the ingress of insects (such appears to be the case with *Polygonum Convolvulus* and *P. hydropiper,* the flowers of which seem to be always closed, and with many others.

He regards existing inconspicuous forms not as primitive, but as derived from conspicuous progenitors, which in turn owed their origin to the selective influence of insects.[9]

It has been shown that Plateau's conclusion is not sustained either by the phylogeny and distribution or by the ecology and manner of fertilization of inconspicuous flowers, which have almost universally been compelled to adopt anemophily or autogamy. In the few exceptional cases there are present other allurements, as odor and nectar, which sooner or later attract insects; but this

[9] Henslow, George, "On the Self-fertilization of Plants," *Trans. Linn. Soc.* (Botany), Ser. 21, 317–398, 1880.

does not prove that cœteris paribus color contrast is not an advantage. No assertion is made that bees have an antipathy to green, only that flowers of this hue are not as readily seen amidst the foliage. Very likely a green flower opposed to red or yellow leaves would attract the attention of insects as readily as the reverse contrast. Following the example of Plateau, I have included the species of *Tilia* among greenish flowers, but it is doubtful whether the inflorescence of the American basswood should be considered as inconspicuous. The flowers are of medium size, sweet scented, produced in vast quantities, and are described by a disinterested observer as "yellow and rather pretty." The nectar is so copious that a single hive of bees has obtained 66 pounds in three days, and its odor is so strongly aromatic that it can be perceived throughout an entire apiary.[10] It may, however, serve as an example of an exceptional species. The importance of scent as an attractive factor was, of course, recognized by Müller, but green flowers are usually odorless, as pointed out by both Hooker and Henslow.[11]

As additional evidence that insects will visit green flowers Plateau describes how he placed honey on seventeen anemophilous flowers, as grasses, sedges, rushes and on species of *Rumex* and *Chenopodium*, and observed visits of honey-bees, flies and a few other insects.[12] He also fashioned crude imitations of flowers from the living leaves of the red currant (*Ribes rubrum*) and the sycamore (*Acer Pseudo-Plantanus*), in which he put

[10] Root, A. I., "The A B C of Bee Culture," p. 397, 1903. A single colony of bees belonging to the late Dr. Gallup, of Orleans, Iowa, once gathered 600 pounds of basswood honey in thirty days. Doolittle, G. M., "Honey from Basswood," *Gleanings in Bee Culture*, 36, 23, 1908.

[11] A nectariferous flower may be both green and scentless and yet be found by bees. According to Fritz Müller the flowers of a species of Trianosperma in South Brazil are visited very abundantly all day long by *Apis mellifica* and species of *Melipona*, although they are scentless, greenish, quite inconspicuous, and to a great extent hidden by the leaves. "The Fertilization of Flowers," p. 270.

[12] Plateau, F., "Comment les fleurs attirent les insectes," *Bull. Acad. roy. Belgique*, 4me partie, 3me série, 34, 602–612, 1897.

honey, and they attracted bees and flies.[13] Attention is also called to the secretion of nectar by extra-floral nectaries upon the petioles of *Prunus*, the stipules of *Vicia* and the leaves of various trees. These sources of sweet secretions are frequently visited by Hymenoptera and other insects, as well as over-ripe or partially decayed fruit.[14]

A more interesting example than any given by Plateau of the secretion of nectar by extra-floral nectaries is furnished by the American cotton plant. Besides the nectar glands within the flowers there is a small gland on the center rib on the under side of each leaf, which at times secretes nectar very freely. When the atmospheric conditions are right, says Mr. J. D. Yancey in a recent number of *Gleanings in Bee Culture*, drops of nectar will collect on these leaf glands so large that they may be readily tasted; and a bee has to visit only a very few to obtain a load.

> At such times they neglect the blossoms entirely, and the honey comes in with a considerable rush. I could not tell that this honey was any different in either color or flavor from that gathered from the blossoms.

No other plant in this country besides cotton is known to me which has extra-floral nectaries, which are of value as a source of honey; but in favorable years there occurs on a scale of enormous magnitude an illustration that honey-bees will readily learn to gather sweet liquids from green leaves. In many parts of Europe and America Aphididæ, or plant-lice, and scale insects (*Lecanium*)[15] excrete a sweet substance called honey-dew in such large quantities that not only the leaves of the trees, but even the grass and the sidewalks, are coated with it as with a varnish. Honey-dew is attractive to many insects, as bees, ants, wasps and flies. In California it is sometimes

[15] In Hawaii enormous quantities of honey-dew are produced by a leaf-hopper. Phillips, E. F., "The Source of Honey-dew," *Gleanings in Bee Culture*, 38, 177, 1910.

[13] *Loc. cit.*, 5me partie, p. 868.

[14] *Loc. cit.*, 4me partie, p. 604.

so abundant that bees gather large stores of it, and Professor Cook says that he has sold it by the barrel.[16] From Sevensville, Montana, a correspondent of *Gleanings in Bee Culture* wrote a few years ago that the honey-dew had been in a continuous flow throughout the whole season, and dripped on the sidewalk every night in large quantities. Another bee-keeper at Dupont, Indiana, states that, in 1884, his bees gathered about two tons of honey-dew from the leaves of the oak, hickory, beech and wild grape. But the year, 1909, was in the opinion of well-informed apiarists the greatest year for honey-dew ever known in America. Bee-keepers everywhere reported a scarcity of white clover and basswood honey and that the bees were storing honey-dew. Professor Surface says:

> I have never known a year in all my studies of entomology, and in a correspondence of thousands of persons each month, during which plant-lice, or aphids, have been so abundant as they have this year (1909), and consequently the honey-dew was likewise unusually abundant.[17]

Many tons of this sweet excretion were consumed by the bees during the following winter.

I have dwelt at some length on the collection of honey-dew in order to establish beyond any question, not only that domestic bees would, but that they do gather large supplies of sweet substances from green leaves. If additional evidence could strengthen this statement it is furnished by every apiary, where bees frequently may be seen feeding on materials of every hue, or entering dark supers, hive-bodies, or boxes, through narrow crevices or small apertures no larger than a bee's body in search of honey. Honey-bees require a great amount of stores and it would be greatly to their disadvantage, if their actions were dominated by bright coloration to such an extent that they were prevented from obtaining food supplies

[16] Root, A. I., and Root, E. R., "The A B C and X Y Z of Bee Culture," p. 273, 1910.

[17] Surface, H. A., "Sources of Honey-dew," *Gleanings in Bee Culture*, 37, 623, 1909.

from every available source. It is, then, freely admitted that bees will collect sweet liquids, after they have once been found, from green or dull-colored surfaces; but this is very far from proving that bright coloring is not an advantage to flowers, and it is astonishing that such a claim based on the above facts should ever have been made.

Knuth in reviewing the observations of Plateau on greenish and brownish flowers very properly raises the objection that "Plateau has not compared the frequency of insect visits to inconspicuous and conspicuous flowers of the same size, and it is only experiments of this kind which can help to settle the point at issue."[18] This omission is fatal to Plateau's argument, and it is difficult to understand why control experiments were not employed. It is the object of the present paper to present the results of a long series of experiments, in which honey-bees under similar conditions were given the choice between a conspicuous and an inconspicuous object.

As a preliminary inquiry it is of interest to determine whether plants with diœcious inflorescence afford any assistance in deciding this question. As is generally known, the staminate flowers of entomophilous and sometimes of anemophilous diclinic species are more conspicuous than the pistillate. This is well shown by the genus *Salix*. Willow branches bearing staminate aments are offered for sale in New England cities in early spring, and are used for decorative purposes in the churches of England on Palm Sunday. Careful observation and collection of the visitors of *Salix discolor* (the glaucous or pussy willow), the earliest species of *Salix* to bloom in this locality, shows that the number of insects attracted by the staminate aments is much greater than by the pistillate. The difference is, indeed, so marked as to be readily apparent to any one who will keep an individual shrub of each form under observation for a few hours.

[18] Knuth, Paul, "Handbuch der Blütenbiologie," 1, 394, 1898; "Handbook of Flower Pollination," translated by J. R. Ainsworth Davis, 1, 207, 1906.

Another common diœcious plant is *Rhus typhina* L. (*Rhus hirta* (L.) Sudw.).[19] The staminate flowers are in large white panicles. The thyrsoid, pistillate flower-clusters are dark green; but as they are terminal and borne well above the foliage they are visible at a long distance, *i. e.,* they have conspicuousness of position. Two large groups of this shrub, or small tree, one of which was pistillate and the other staminate, growing in an open woodland only a short distance apart, were selected for observation. During two collecting trips in July, 1909, I secured on the staminate blossoms 77 visitors, but only 6 on the pistillate. Of the visitors to the staminate flowers 63 were bees, 2 wasps, 2 flies, 8 beetles and 2 Hemiptera. Of the visitors to the pistillate flowers 4 were bees and 2 wasps. Even a brief inspection is sufficient to show that the staminate flowers are more attractive to insects than the pistillate.

The staminate inflorescence of *Salix discolor* and *Rhus typhina* is, then, undoubtedly more conspicuous and attractive to insects than the pistillate; but is this larger company of visitors due wholly to its brighter coloration? Evidently not. Great numbers of honey-bees and many species of *Andrena* frequent the staminate aments of *Salix* to procure pollen for brood-rearing. At least five species of *Andrena* are oligotropic visitors of this genus. Examination of the polleniferous scopa of the bees taken on the staminate flowers of *Rhus typhina* showed that they all contained pollen except nine specimens of *Prosopis* (*P. modesta* Say and *P. piziœ* Rob.), a primitive genus, the species of which possess only feebly developed brushes on the posterior legs, which are not used for carrying pollen. Of the eight species of beetles taken on the staminate flowers microscopic examination showed an abundance of pollen on the mouth-parts of four. The other four beetles were of small size, and it was not definitely determined whether they or the other insects mentioned above were feeding on pollen or not. But this

[19] The flowers of *Rhus typhina* are given as polygamous in most plant manuals, but they are certainly diœcious, as is also stated by Müller.

was of little consequence, since the proof is ample that in the case of the staminate plants of *Rhus typhina,* as in *Salix,* the pollen is an important factor in attracting visitors.

It is commonly believed that insects are attracted first to the staminate flowers of entomophilous diœcious plants by their greater conspicuousness, from which subsequently they carry pollen to the pistillate flowers. For instance, Müller says of the diœcious flowers of *Asparagus officinalis:* "This instance confirms Sprengel's oft-repeated rule that the male flowers of diclinic plants are more conspicuous than the female, whence insects are likely to visit the two kinds of flowers in their proper sequence."[20] But it is clear that many insects never fly to the pistillate flowers, since if they did the number of visitors to the two kinds of flowers would be equal. This is especially true of female bees, which, having obtained their load of pollen, often return directly to the hive or nest. Of the four bees taken on the pistillate flowers of *Rhus typhina* only two had pollen on the scopa of the hind legs. After collecting the pollinators of this species for several seasons I think it probable that some of the species of bees taken on the staminate flowers are never, or very rarely, found on the pistillate blossoms.[21] Sprengel's rule must, therefore, be accepted with considerable reservation.

The observations on diœcious flowers not proving well adapted for the purpose intended, owing to the presence of pollen as an attractive factor, the following experiment was tried. The flowers of *Gerardia purpurea* have a rose-colored, campanulate corolla and a short bell-shaped calyx. The species is common in this locality and is sparingly visited by bumblebees. When a large bouquet of the flowers was placed in front of a hive of black bees, it received very little attention. Apparently they contained no nectar. I now placed in the throat of a

[20] Müller, H., "The Fertilization of Flowers," p. 549.

[21] This is also true of dichogamous flowers. Robertson, C., "Flowers and Insects," *Bot. Gaz.*, 27, 41, 1899.

large number of flowers a small drop of honey. From a number of other stems I removed all the corollas and all conspicuous buds, and between the green calyx teeth I also put a drop of honey. So abundant was the honey on the green calyces that it could be seen at a distance of four feet. I could detect no scent in the complete flowers; certainly they seem to possess none comparable with that of honey. The two clusters of plants, the one decorallated and the other with its flowers complete, were placed on opposite sides of a glass of water, which was set near the entrance of a hive of black bees. The bees immediately showed a decided preference for the flowers retaining their corollas, as many as five visiting them at one time; while there were no bees on the denuded flowers though they were on the side of the glass nearer the hive. Later the bees discovered, as was to be expected, the honey on the green calyces and removed it. It is evident that to place honey on small green flowers, as in the experiments of Plateau with grasses and sedges, and when it is finally found by insects to conclude that conspicuousness is not an advantage is unjustifiable. The bees gave a decided preference to the brighter-colored flowers, and the fact that they subsequently discovered and removed the honey from the green calyces furnishes no evidence whatever against the benefit of color contrast.

But a method of experimenting was wanted, which would permit of varying the conditions under which the conspicuous and inconspicuous objects were exposed, and of counting the number of visits to each. This was obtained in the following manner: A small number of honey-bees were trained to visit for honey an unpainted, dull-gray board raised upon a support two feet high. A short time before the honey, which was placed directly on the board, was wholly removed, a conspicuous and an inconspicuous object were placed at equal distances from the board and at a known distance from each other. As soon as the bees had consumed the honey they began describing a series of ever widening circles in search of a new supply until one or both of the above-mentioned

objects were discovered. The number of visits made to each in a given time was then counted, and served as a basis for estimating numerically the value of conspicuousness.

On October 1, 1909, a small number of bees were accustomed to visit the dull-gray board, on which there was a small quantity of honey. For convenience this board will be called the feeder. While the bees were busily at work, I put a blue slide (prepared by placing the floral leaves of the bee larkspur (*Delphinium elatum*) between two glass object slides, 3 × 1 in.), on the center of which there were a few drops of honey, on the grass of the lawn about three feet from the base of the feeder; and on a dandelion leaf three feet from the base of the feeder and five feet from the blue slide honey was also placed. As soon as the supply of honey on the feeder was exhausted the bees began circling in the air. In a few minutes one bee had found the blue slide, in ten minutes two bees, and in twenty-five minutes five bees; but none had found the honey on the dandelion leaf. I now placed beside the dandelion leaf an apple leaf with a comparatively large quantity of honey on it, and at the end of forty minutes one bee found it and a little later a second bee. I doubt if they would have found it then had they not for some time previously been flying low searching for honey in the grass, having from their previous experience with the blue slide learned to look for it there. In this experiment the advantage was clearly on the side of the conspicuous object. It would appear that if two flowers were blooming at some distance apart, the one bright colored and the other green, the former would be the more likely to be pollinated.

On October 3, at 12:33 P.M., I repeated this experiment. The blue slide, a dandelion leaf, both on the grass, and the base of the feeder formed the angles of an equilateral triangle, each side of which was three feet. Honey was placed on all three as before. Two minutes after the last drop of honey on the feeder had disappeared three Italian

bees found the blue slide. At 12:40 there were eight bees on the blue slide, but not one had found the honey on the dandelion leaf. Five minutes later there was one bee on the leaf.

If bees are guided by odor exclusively in their search for nectar, and contrast in color with green foliage is no advantage to flowers, then it would seem as though they should find a quantity of free honey as readily as when it is associated with bright coloration. About thirty Italian bees were accustomed to visit the gray-colored board, or feeder, which, as previously stated, rested upon a support two feet high. Six feet from this support and six feet apart, the three forming an equilateral triangle, were placed two poles each $4\frac{1}{2}$ feet high. On top of one of the poles was placed a quantity of honey so large that it ran down on the side, and was visible at a distance of twenty feet. To the top of the other pole was attached a cluster of yellow "immortelles" (*Helichrysum bracteatum*) gathered many years ago, and which appeared to be absolutely devoid of scent. Each of the flowers was about $1\frac{1}{4}$ inches in diameter and the cluster was 3 inches long by three inches wide. At 11:10 A.M., the bees were permitted to consume all the honey on the feeding board. In three minutes there were three bees and one fly on the flowers, but no insects had found the free honey. In five minutes there were four bees and one fly on the flowers, and one bee on the free honey. At 11:20 the latter bee left for the hive and five minutes later returned; a second bee also alighted on the side of the pole and began sucking the honey which had run down from above; two flies, apparently house flies, also came. At the same time there were six Italian bees on the flowers. At 11:30 A. M., there were six Italian bees and one fly on the flowers, but only one bee on the free honey. The flowers not only attracted the bees earlier than the free honey, but three times as many of them.

I now transposed the poles. But to the top of the pole on which there had previously been the supply of free

honey I fastened a single yellow "immortelle" one inch across. The individual flower enjoyed the advantage of position since it stood where the cluster had been before. Honey was placed on all the flowers. At 11:50 A.M., there were nine Italian bees and a Syrphid fly on the cluster of flowers and three Italian bees and one fly on the single flower. The larger and more conspicuous object notwithstanding its changed position received the greater number of visitors.[22]

The following experiments were made in 1910, and only black bees were employed. As in the experiments of the preceding year, the bees were trained to visit the same dull gray board placed upon a support two feet high. On September 14, 1910, at 12:40 P.M., the bees were carrying away syrup of sugar from the feeder. Nine feet from its base I put out on the grass of the lawn a dried yellow flower of *Helichrysum bracteatum* $1\frac{1}{4}$ inches in diameter, containing a small quantity of honey. On the opposite side of the feeder at a distance of nine feet from its base I laid a Red Astrachan apple leaf, 2 inches long by $1\frac{1}{2}$ wide, on the center of which there was an ample supply of honey. There were at least twenty-five bees on the board and later the number increased. At 12:55 they had wholly consumed the sugar syrup. At 1:07 a bee came to the flower, but left almost immediately. At 1:10 a second bee came to the flower, but soon left, and a few moments later a third visit was made in the same way. No bees had found the leaf. As the honey was excellent I could account for the brief stop made by the bees only on the ground that they were looking for sugar syrup. In the next experiment this was offered to them.

At 1:20 P.M., I again put sugar syrup on the feeder, and removed the flower and leaf from the grass. Another "immortelle" $1\frac{1}{4}$ ins. in diameter and another Red Astrachan apple leaf, 2 inches long by $1\frac{1}{2}$ inches wide, were laid on the grass on directly opposite sides of the feeder,

[22] Cf. Müller's remarks on *Geranium, Epilobium, Polygonum* and the Alsineæ.

but six feet instead of nine feet away from its base. The leaf was on the same side as before, as was also the flower. Sugar syrup, which is odorless, was placed on each. At 1:30 the bees finished the syrup on the feeder. One bee flew almost immediately to the flower, but made a brief stay. At 1:34 a second bee came and sucked, and three minutes later a third bee came. No bees had found the leaf.

Sugar syrup was again put on the feeder, and the flower and leaf were moved three feet nearer its base, each now being distant three feet. At 1:47 the syrup on the feeder was all consumed, but even previously one bee had come to the flower. At 1:47 a bee flew over the leaf, but did not alight. At 1:50 three bees came to the flower, and a moment later a fourth, and afterwards two more. At 2 P.M., there were three bees on the flower, a fourth came a little later and then a fifth. No bees had visited the leaf.

Syrup of sugar was again placed on the feeder. At 2:5 P.M., I put out the yellow flower and apple leaf used in the first experiment. On these, it will be remembered, honey had been placed. They were laid on the grass on opposite sides of the feeder, each three feet distant from its base. At 2:10 the sugar syrup on the feeder was all removed. A bee soon came to the flower, but did not stop, a second bee came and sucked, a third bee came, but did not stop, several bees came but did not stop; but at 2:13 there were three bees sucking honey on the flower. A bee flew slowly over the leaf I thought it would certainly be attracted by the scent of the honey, but this was not the case. The experiment was continued a little longer and one or two more visits were made to the flower, but none to the leaf.

The results obtained in the four preceding experiments are deserving of careful attention. While the yellow flower containing honey and the one containing scentless sugar syrup were visited many times by bees, the leaves remained wholly unvisited, though the supply of syrup

or honey on them was plainly visible at a considerable distance. According to the reiterated statement of Plateau all flowers might be as green as their leaves without their pollination being compromised, and color and form are of little consequence in comparison with odor. But the experiments showed that color contrast is of great value, and in these particular experiments indispensable. If the leaves provided with an ample supply of honey or syrup could not obtain a single visit under the conditions described, where a large number of bees were brought into their immediate vicinity, how little chance there would be for an isolated plant with small green flowers growing in a secluded location attracting visitors! But a bright-colored flower in the same locality would be much more likely to gain the attention of pollinating insects.

On September 20, 1910, at 2:15 P.M., numerous black bees were coming to the feeder for honey. At a distance of three feet away I laid on the grass a bright yellow flower of golden glow (*Rudbeckia laciniata*) two inches in diameter. On the opposite side of the feeder three feet from its base, I laid the end of a spike of *Amarantus retroflexus* about three inches long. The small, pale green flowers are thickly crowded in panicled spikes. An ample supply of honey was placed on both. In the course of fifteen minutes there were 18 visits to the flower of golden glow and only 8 to the *Amarantus* cluster. If a bee flew to either object, but did not alight because of the large number of bees already there, this was counted as a visit.

The bees were again accustomed to visit the feeder. In the preceding experiment one of the objects had been placed on the east side of the feeder and the other on the west. Both the flower of the golden glow and the spike of *Amarantus* were now laid side by side on the grass in the sunshine three feet to the north of the feeder. There was honey on both. In less than ten minutes there were fifteen visits to the golden glow and only three to the

spike of *Amarantus*. At one time there were five bees on the golden glow and only two on the spike of *Amarantus*.

At 2:45 P.M., I repeated the preceding experiment, but I placed the flower of the golden glow and the spike of *Amarantus* on the south side of the feeder three feet from its base, but only three inches apart. Honey was put on both at the beginning of the experiment. In ten minutes there were 18 visits to the golden glow and 5 to the green spike of *Amarantus*. At one time there were four bees on the flower of golden glow, but only one on the spike of *Amarantus*. It often happens when a bee comes to a flower on which one or more bees are already at work that they will all fly up in the air and then all or in part settle down again. Such flights were not counted. Frequently a bee flew directly to the golden glow as though it had been seen from a distance.

It will be remembered that Plateau put honey on the green inflorescence of several species of *Chenopodium*, besides other anemophilous flowers, and when it was found by insects reasserted his oft-repeated conclusion that winged pollinators are guided to flowers almost exclusively by odor and that color contrast is of little value. Plateau employed no control experiments, but it appears from the experiments just described that though the odor of the honey drew insects to the green inflorescence, nevertheless it was at a disadvantage because of the absence of bright coloration.

In several of the experiments of 1909 a blue slide was used, prepared by placing the leaves of the perianth of the bee larkspur (*Delphinium elatum*) between two glass object slides tied firmly together with black silk. It might perhaps be objected that the scent of these floral leaves would escape through the narrow crack between the two glass slides. While I think this improbable, and that in any event it would be so slight as to bear no comparison with that of the honey placed upon the upper glass slip and, therefore, would exert no influence on the

behavior of the bees, still it seemed desirable to test the matter. For this purpose the following experiment, closing the series of 1910, was performed on September 23. A blue slide was prepared as described and the edges were sealed with several applications of gold size, the odor of which is no doubt unpleasant to bees. The blue slide, a dandelion leaf, and the base of the feeder formed the angles of an equilateral triangle, each side being three feet in length. As the weather was becoming colder the bees were not flying freely. An ample supply of honey was put on the blue slide and the leaf, which were laid on the grass of the lawn at 9 P.M. At 9:20 the honey on the feeder was entirely consumed. Presently a bee hovered over the blue slide, but did not alight. Another bee hovered over the blue slide for a long time and finally alighted. A second, third and fourth visit was made by bees at intervals. At 9:40 I discontinued the experiment. No attention had been paid to the honey on the leaf, though in the sunlight it could be seen for a long distance. The hesitation of the bees at first may have been caused by the repellent odor of the gold size. Beekeepers never paint their hives inside, as the scent of paint is believed to be disliked by bees. The blue slide and the leaf were left in position and when twenty minutes later I examined them again all of the honey had been removed from the slide, but that on the leaf appeared to be untouched. Evidently the only factors which had influenced the bees in the previous experiments were the honey and the color.

Of the series of experiments performed in 1911 only three will be described. A few observations were thought desirable in which one or two bees were employed instead of a larger number, in order that the behavior of an individual bee might be followed when given the choice between a conspicuous and an inconspicuous object. A few bees were accustomed to visit a glass slide for honey. While they were absent at the hive, the slide was removed and a large rhubarb leaf was laid in its place.

About two inches from the base of the leaf there was put a quantity of amber-colored honey sufficiently large to form an oval mass, which could be seen in the shade at a distance of twenty feet. Twelve inches from the honey and a few inches from the apex of the rhubarb leaf there was placed a bright red flower of the Zanzibar balsam (*Impatiens sultani*), an inch in diameter, on which there was a small amount of honey.

A bee returning from the hive went directly to the red flower, where it took up its load and flew away.

A bee came to the red flower. Two more bees came and were impounded. The first bee left for the hive.

A bee returned to the flower. A second bee came, both flew up in the air, and one of them went to the mass of honey but soon returned to the flower. The first bee left for the hive. I attempted to impound the second, but it escaped.

A bee came to the flower, and after five minutes returned to the hive.

The bee returned to the flower. A second bee came, and hovered in the air for some time, but finally settled by the bee on the flower. Both bees left for the hive. Both bees returned to the flower, and when they again left I discontinued the experiment. The rhubarb leaf was removed and the bees were given honey on a glass slide.

It seems impossible to explain the behavior of the bees in this experiment on the supposition that they were guided chiefly by odor. In view of the large quantity of honey and its easy accessibility there would have been no occasion for surprise had the bees given it much greater attention.

After carefully removing the honey from the rhubarb leaf I placed near its apical end four flowers of the Zanzibar balsam, forming a bright red square. On one petal of each flower there was a small drop of honey. Ten inches away near the base of the rhubarb leaf I put a single petal of a balsam flower on which there was a large drop of honey. While both bees were away I removed the

glass slide and substituted the rhubarb leaf, reversing its position, however, so that the small object was where the larger had been before.

Both bees returned to the cluster of four balsam flowers. One of them presently flew over to the single petal, but soon returned to the cluster; later it again went to the petal and again returned. Both bees left for the hive.

A bee returned to the cluster, did not alight, but flew over to the petal and sucked. When the second bee returned it disturbed the bee on the red petal, and both went to the cluster. One of the bees left for the hive.

A bee came from the hive to the cluster. One of the bees then flew over to the petal but did not alight, returned to the cluster. Both bees left for the hive.

Both bees returned to the cluster. One of them left for the hive and on its return went to the petal. The bee on the cluster left for the hive.

While the cluster of four red flowers received the greater number of visits, as would be expected, more attention was given to the drop of honey associated with a red petal than was received by the larger oval mass of honey alone in the preceding experiment.

In a series of interesting experiments with cotton flowers where the visitors were chiefly a species of *Melissodes* (*M. bimaculata*), recently described by Allard, it was observed that when a flower was partially screened by leaves the attention it received decreased; and when the petals were masked on both sides with sections of green leaves the flower was ignored entirely.[23] This result was confirmed by the following experiment. On a cloudy, windy day while a number of black bees were visiting the feeder for honey, I placed on the grass two red flowers of the Zanzibar balsam; each was five feet from the base of the feeder and their distance apart was

[23] Allard, H. A., "Some Experimental Observations concerning the behavior of Various Bees in their Visits to Cotton Blossoms," AMER. NAT., 45, 615 and 672, 1911.

two feet. There was a small quantity of honey on both. One of these blossoms I screened with dandelion leaves on the side toward the feeder, but it was visible in every other direction. Some time after the honey was all consumed on the feeder two bees flew over the unconcealed flower but did not alight. A wasp (*Vespula victua* Sauss.)[24] found it and at the end of half an hour it was visited by a bee. The partially concealed flower received no attention. During this experiment the bees seldom inspected objects on the lawn though they frequently flew to where I was sitting, ten feet away.

The conclusion derived from a study of the phylogeny, ecology, distribution and fertilization of green flowers that they are at a disadvantage in attracting insects be cause of their color was fully sustained by a long series of experiments, in which honey-bees were given the choice between a green and a bright colored object placed on a green background, or between a conspicuous and an inconspicuous object. In the experiments described both black and Italian bees were employed, the number of which varied from one to fifty. The observations extended over portions of three seasons. Conspicuous and inconspicuous objects were in some instances placed diametrically opposite to each other at varying distances, in other cases side by side or a few feet apart. In six experiments there were no visits to the inconspicuous object; while in the other experiments the number of visits to the conspicuous object was much larger than to the inconspicuous object, usually twice or three times as large. The theory that bees in gathering nectar are influenced only by the olfactory sense and not by color or form does not afford a satisfactory explanation of the facts presented. If, however, bees are guided by the sense of vision as well as by that of smell, then their relations both past and present to green flowers are not difficult to understand. To reject a natural and wholly

[24] For the determination of this species I am indebted to Mr. S. A. Rohwer.

satisfactory explanation of their behavior in favor of an improbable hypothesis has the appearance of shunning the truth in a vain search for novelty.

Conclusions

Green flowers are not well adapted to entomophily, and many species, possibly all, have been derived by retrogression and degeneration from larger more highly developed entomophilous forms. They are usually small, or even minute, and are often incomplete, while anemophily and autogamy prevail. Entomophilous green flowers are as a whole sparingly visited by insects belonging to the less specialized families, and as a rule retain the power of self-fertilization.

The fact that insects have been observed feeding on over-ripe or decaying fruit, or the glandular secretions of the vegetative organs of plants, or the excretions of Aphididæ on foliage, or greenish or brownish flowers, or dull-colored receptacles which have contained sugar or sweet liquids, affords no evidence that conspicuousness is not an advantage to entomophilous flowers. Any surface, whether it is bright or dull-colored, on which there is nectar or honey, will be freely visited by bees for stores after these liquids have once been discovered; but they will not be discovered as quickly on a surface which does not contrast in hue with its surroundings as on one which does so contrast.

The experiments and observations of Plateau on green or greenish flowers in the absence of control or comparative observations are fallacious, as pointed out by Knuth, and do not prove that "all flowers might be as green as their leaves without their pollination being compromised."

When honey-bees are given the choice between a conspicuous and an inconspicuous object under similar conditions, they exhibit a preference for the former. This preference is sufficiently marked to account for the development of color contrast in flowers.